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Pinus prekesiya sp. nov. from the upper Miocene of Yunnan, southwestern China and its biogeographical implications

Yaowu Xing [a,b], Yu-Sheng (Christopher) Liu [c,*], Tao Su [a,b], Frédéric M.B. Jacques [a], Zhekun Zhou [a,*]

[a] *Key Laboratory of Biogeography and Biodiversity, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming 650204, China*
[b] *Graduate University of Chinese Academy of Sciences, Beijing 100049, China*
[c] *Department of Biological Sciences, Box 70703, East Tennessee State University, Johnson City, TN 37614-1710, USA*

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ABSTRACT

Pinus prekesiya Xing, Liu et Zhou sp. nov. was described as a new species on the basis of two well preserved ovulate cones from the upper Miocene of central Yunnan, southwestern China. It is the first fossil record of three dimensionally preserved *Pinus* ovulate cones from China. Morphological comparisons with 15 previously published Cenozoic cones and seven related extant pine species reveal that the fossil cones are identified as a new species, *P. prekesiya* sp. nov., which belongs to subsection *Pinus* of subgenus *Pinus*. The new species shows a combination of characters of *P. kesiya* and *P. yunnanensis*, but has a closer affinity with *P. kesiya* which occurs in the humid region of Yunnan and therefore suggests a more humid climate in central Yunnan during the late Miocene than today. The general cooling trend during the late Neogene and topographic change due to the dramatic Tibetan uplift might have caused a vicariant origin of *P. kesiya* and *P. yunnanensis* from the ancestral *P. prekesiya*.

1. Introduction

Pinus L. is the largest genus of Pinaceae with about 110 extant species occurring throughout the Northern Hemisphere (Critchfield and Little, 1966; Fu et al., 1999). Its natural distribution ranges from the Arctic and subarctic regions of North America and Eurasia to the subtropical and tropical regions of Central America and Asia, with only one species, *P. merkusii* Jungh. & de Vriese, extending south of the equator in Sumatra (Critchfield and Little, 1966; Mirov, 1967; Price et al., 1998). *Pinus* is often a dominant component of vegetation in large parts of the Northern Hemisphere (Richardson and Rundel, 1998). Because of its great ecological importance, the systematics and evolution of this genus have received considerable attention (Price et al., 1998).

The genus *Pinus* is in general well represented in the fossil record although the fossil occurrence is not balanced (Gaussen, 1960; Axelrod, 1986; Mai, 1986; Klaus, 1989; Millar, 1998). Most of them are vegetative remains, such as wood and leaves, which provide limited information in systematics, while reproductive organs are crucial for good determination at the section or even subsection level, but unfortunately they are very rare, those from the European browncoal sediments excepted (Smith and Stockey, 2002). Alvin (1960) described a permineralized cone, *Pinus belgica* Alvin, from the early Cretaceous Wealden Formation of Belgium. This is the oldest confirmed fossil record of *Pinus*. Up till now, more than 30 species, most of which represent permineralized or coalified cones from the Cretaceous to Neogene, have been recognized and studied in detail (Chaney, 1954; Miller, 1969, 1973, 1974, 1978, 1992; Tao and Kong, 1973; Robinson, 1977; Underwood and Miller, 1980; Banks et al., 1981; NIGMR, 1982; Stockey, 1983, 1984; Tao and Wang, 1983; Mai, 1986; Miller and Malinky, 1986; Stockey and Nishida, 1986; Klaus, 1989; Saiki, 1996; McKown et al., 2002; Smith and Stockey, 2002; Erwin and Schorn, 2006). Axelrod (1986) reviewed Cenozoic history of the American pines and discussed their evolution in relation to environmental change; while in Europe, Mai (1986) and Klaus (1989) reviewed the European fossil *Pinus* and the history of Mediterranean pines based on the seed cones morphology (e.g. apophysis and umbo). Based on her extensive review of fossil pines in the Northern Hemisphere, Millar (1998) discussed the early evolution of pines. The fossil evidence, together with phylogenetic analyses of extant taxa, has greatly contributed to our knowledge of *Pinus* evolution (Millar, 1998; Price et al., 1998; Eckert and Hall, 2006). Biogeographically, a region that underwent intensive mountain-building events often became a secondary center for pine radiations (Millar, 1998). Situated in southwestern China, Yunnan province had experienced strong influence of the uplift of the Tibetan Plateau during the late Cenozoic and is now recognized as one of the major secondary

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* Corresponding authors. Tel./fax: +86 871 5219932.
E-mail addresses: liuc@etsu.edu (Y.-S.(C.) Liu), zhouzk@mail.kib.ac.cn (Z. Zhou).

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diversification centers of extant pines (Fu et al., 1999). Although the Neogene pollen record of *Pinus* in Yunnan is abundant (Tao and Du, 1982; Wang, 1996; Xu et al., 2000; Wang and Shu, 2004), only one species of pine cone, cf. *P. yunnanensis* Franchet, has been previously reported (Tao and Kong, 1973). Unfortunately, due to the poor preservation of this fossil, no detailed comparisons were carried out (Tao and Kong, 1973).

The fossils described in this study are the first three dimensionally coalified pine cones from China. Therefore, they are of great importance for further understanding of *Pinus* evolution during the Neogene in Southwest China. Also, the present fossil pine cones enable us to test the hypotheses of Millar (1998) concerning the Cenozoic evolution of pines. The main purposes of the present paper are first to study the taxonomy of the fossil cones through comparisons with selected extant and fossil pine cones, and secondly to discuss their biogeographic implications.

2. Material and methods

The two fossil cones were collected from the Xiaolongtan Formation, exposed in Xianfeng Coalmine (Fig. 1; 25°25′ N, 102°51′ E, Elevation 2200 m), located about 60 km north of Kunming, the capital city of Yunnan Province, southwestern China (Fig. 1). The geological age of the Xiaolongtan Formation has been considered to be part of the late Miocene according to mammal fauna (Zhang, 1974; Dong, 2001), plant and pollen assemblages (Zhou, 1985, 2000; Wang, 1996). Based on the lithological sequence, this formation is composed of four members, named as N_1^1x–N_1^4x, respectively (Fig. 2; Xing et al., 1999; Wu et al., 2006). The third member is further subdivided into two sub-members as $N_1^3x^1$ and $N_1^3x^2$ in ascending order (Fig. 2; Xing et al., 1999; Wu et al., 2006). The coalified fossil cones were found in the layer of $N_1^3x^2$, which also yielded abundant plant macrofossils and insect fragments. A preliminary classification on these specimens shows that Fagaceae, Lauraceae, and Fabaceae are dominant in this flora. There are only two types of conifer fossils in the flora, represented by the two pine cones and one hemlock (*Tsuga*) cone. Among the pine cones, one is well preserved and therefore is designated as the holotype. This specimen is a three-dimensional compression, which is not totally adpressed so that it was easily removed from the matrix. The excellent preservation of this specimen enables us to examine both sides of the cone, a rare case for fossil plants.

The fossil cones were carefully washed in distilled water and air-dried. For a detailed comparison, two morphologically closed extant pines, *P. kesiya* Royle ex Gordon and *P. yunnanensis,* were selected. Both the fossil and extant cones were photographed using Canon PowerShot S5 IS digital camera.

The terminology for morphological description of *Pinus* cones follows Klaus (1980, 1989) and Mai (1986), some terms are also illustrated in Fig. 3. The classification system of *Pinus* follows Price et al. (1998), simply because Millar (1998) based her hypothesis of *Pinus* evolution on this system. In the genus *Pinus*, Price et al. (1998) recognize two subgenera, viz. the subgenus *Pinus*, also known as *Diploxylon* or hard pines and the subgenus *Strobus*, also known as *Haploxylon* or soft pines. Subgenus *Pinus* includes two sections (group), Sect. *Pinus* and New world diploxylon pines. The Sect. *Pinus* is subdivided into four subsections Subsect. *Pinus* Loudon, Subsect. *Canarienses* Loudon, Subsect. *Halepenses* Van der Burgh and Subsect. *Pineae* Little and Critchfield. The present fossil pine cones are identified as a member of the section *Pinus* of the subgenus *Pinus*. All the specimens of fossil and living comparatives are housed in the Herbarium of the Kunming Institute of Botany, Chinese Academy of Sciences.

3. Results

3.1. Systematics

Family: Pinaceae Lindley, 1836
Genus: *Pinus* L., 1753
Subgenus: *Pinus* L., 1753
Section: *Pinus* sensu Price, Liston and Strauss, 1998
Subsection: *Pinus* sensu Price, Liston and Strauss, 1998
Species: *Pinus prekesiya* sp. nov. Xing, Liu et Zhou (Plate I, 1–6)
Specific diagnosis: Ovulate cones ovoid-conical, symmetrical, apex tapered. About fifty cone-scale complexes helically arranged, apophyses rhomboid to pyramidal, vallate in plane, bearing numerous ridges radiating out from a centrally located umbo, a distinct

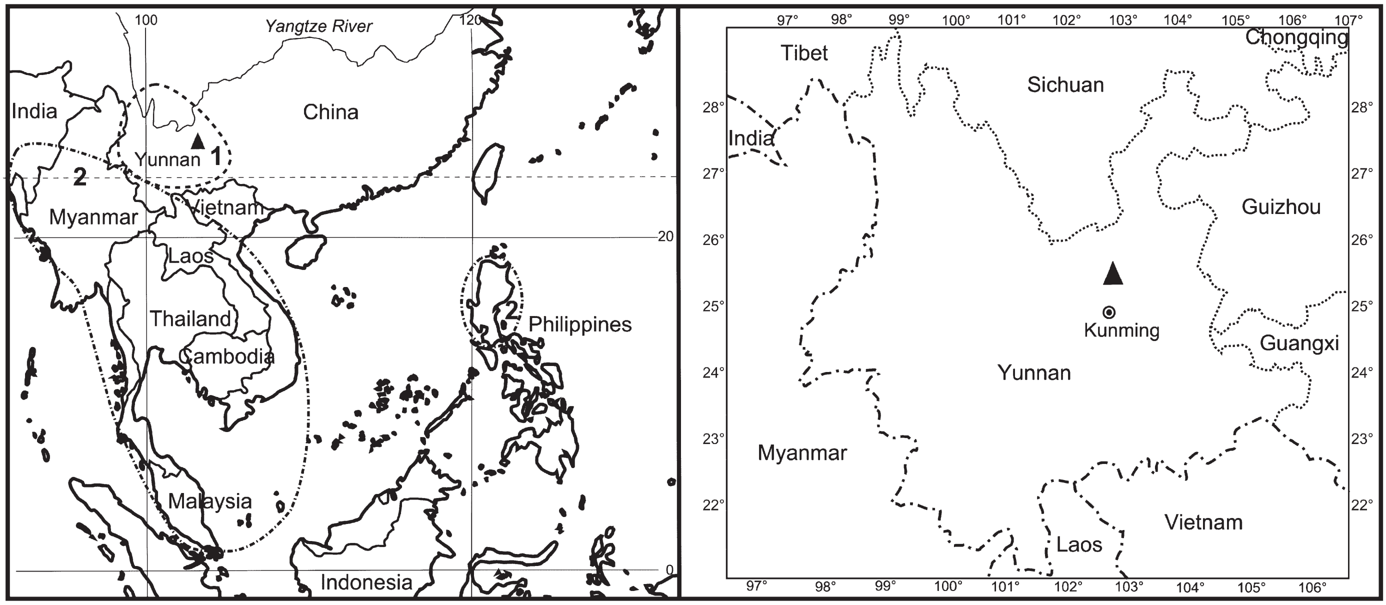
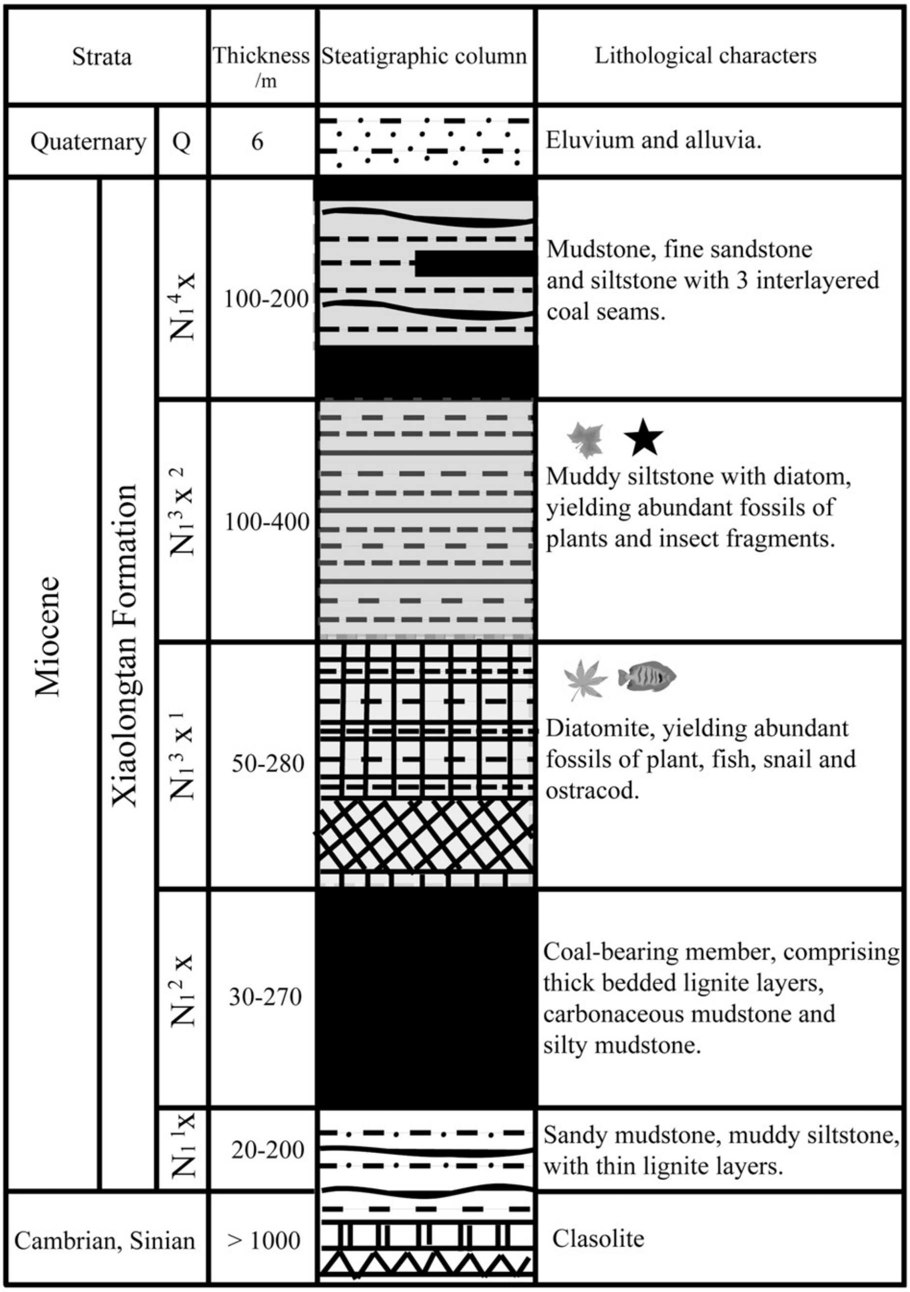


Fig. 1. Map showing the fossil locality (black triangle) of *Pinus prekesiya* sp. nov. (right) and the distribution of *Pinus yunnanensis* (1) and *Pinus kesiya* (2) (left), two closely related extant pines.



Strata			Thickness /m	Steatigraphic column	Lithological characters
Quaternary		Q	6		Eluvium and alluvia.
Miocene	Xiaolongtan Formation	$N_1{}^4x$	100-200		Mudstone, fine sandstone and siltstone with 3 interlayered coal seams.
		$N_1{}^3x^2$	100-400		🍁 ★ Muddy siltstone with diatom, yielding abundant fossils of plants and insect fragments.
		$N_1{}^3x^1$	50-280		🍁 🐟 Diatomite, yielding abundant fossils of plant, fish, snail and ostracod.
		$N_1{}^2x$	30-270		Coal-bearing member, comprising thick bedded lignite layers, carbonaceous mudstone and silty mudstone.
		$N_1{}^1x$	20-200		Sandy mudstone, muddy siltstone, with thin lignite layers.
Cambrian, Sinian			> 1000		Clasolite

Fig. 2. The sketch strata table of the Xianfeng coalmine (simplified after the data of Xing et al., 1999; Wu et al., 2006). The member where the fossils cones were collected is marked as pentagram.

transverse keel, and an obvious sealing band on the lower side of each apophysis. Umbos dorsal, elliptic, slightly sunken, perexcentromucronate, with mucro short and erect. Bract minute.

Etymology: The specific epithet refers to the similarity with the extant species *P. kesiya*.

Holotype: HLT 001A, B (Plate I, 1–5).

Paratype: HLT 002 (Plate I, 6).

Type locality: Xianfeng coalmine (25°25′ N, 102°51′ E), about 60 km north of Kunming, Yunnan Province, China.

Horizon: The upper sub-member ($N_1^3x^2$) of the third member of the Xiaolongtan Formation.

Age: late Miocene.

Repository: Herbarium of the Kunming Institute of Botany, Chinese Academy of Sciences.

3.2. Description

The cones of *P. prekesiya* are ovoid to conical, closed, symmetric, 6.0–7.7 cm long, 3.0–3.5 cm wide, with a tapered apex (Plate I, 1–3). About fifty woody ovuliferous scales, helically arranged around the axis, are preserved per cone. These scales are 1.8–3.5 cm long and 1.0–1.2 cm wide and expanded at each apophysis (Plate I, 1–6). In plane view, basal apophyses are vallate, broadly rhombic, almost pyramidal, 1.1–1.5 cm wide, 1.0–1.2 cm high, and bear an evident transverse keel (Plate I, 1, 2, 4, 6), while apical apophyses are long rhombic, 1.5–1.8 cm long, 0.8–1.0 cm wide and obviously transversely and radially ridged (Plate I, 4, 5). Each apophysis possesses an obvious sealing band, located along the lower sides of the apophysis (Fig. 3; Plate I, 4). The umbos are dorsal, elliptic in plane view, 2.5–4 mm wide, 2–3 mm

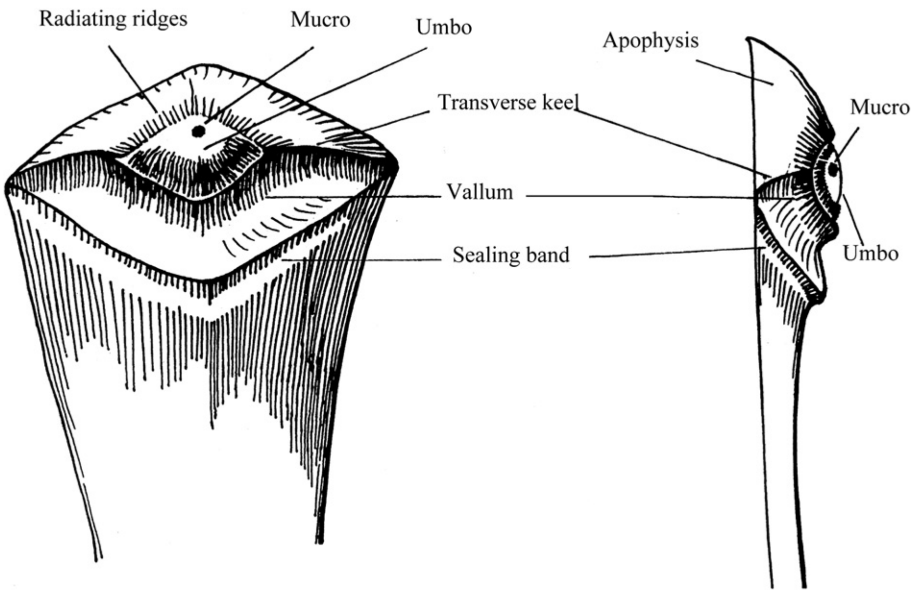


Fig. 3. Schematic figure showing key morphological features of a *Pinus* ovulate cone scale in both dorsal (left) and lateral (right) view (after Klaus 1980, 1989; Mai 1986; Frankis 2002).

high, and slightly sunken (Fig. 3; Plate I, 4, 5). A short mucro occurs on the upper field of the umbo (Fig. 3; Plate I, 4, 5), characteristic of the perexcentromucronate umbo type.

4. Discussions

4.1. Comparisons

The two fossil cones described in the present study are considered to represent the same species due to morphological similarities of the cone-scale complexes and the overall size of the cones. The fossil cones are characterized by the following features: helically arranged cone-scale complexes (Plate I, 1, 2, 6) and ovuliferous scales expanded at apex with an apophysis and umbo (Plate I, 1–6). Because of these features the fossil cones can be assigned to the genus *Pinus* (Miller, 1976). Furthermore, the presence of a dorsal umbo with an evident sealing band (Fig. 3; Plate I, 4) is diagnostic of the subgenus *Pinus* as defined by Frankis (2002).

It is well documented that the combination of morphological characters of umbos and apophyses is often taxonomically diagnostic in *Pinus* infrageneric delimitations (Klaus, 1980, 1989; Mai, 1986; Price et al., 1998). Based on the location of umbos on apophyses, Klaus (1980, 1989) recognized two groups in *Pinus*, in accordance with the traditional classification systems. The first group has terminal umbos, a type present mainly in section *Strobus* of subgenus *Strobus* (haploxylon or soft pines), while the majority of pines have their umbos on the dorsal surface of apophyses. This dorsal umbo type occurs in all the members of subgenus *Pinus* (diploxylon or hard pines) and another section (sect. *Parrya*) of subgenus *Strobus*.

As discussed above, the presence of the sealing band on the lower sides of apophyses exclude closed relationships between the fossil cones described here and the subgenus *Strobus* (Frankis, 2002). Based on the location of mucros on umbos, Klaus (1980, 1989) further subdivided the subgenus *Pinus* into two different groups, i.e. centromucronate and excentromucronate. In the centromucronate umbo type, the mucro is located in the center of umbo, while in the excentromucronate umbo type, the mucro is situated above the transverse keel. Centromucronate umbos are often present in the American pines of the subgenus *Pinus* and excentromucronate umbos occur in all the Eurasian pines of the subgenus *Pinus* (Klaus, 1989). As described above, *P. prekesiya* is clearly excentromucronate. According to the detailed characters of excentromucronate mucros, e.g. size, location, and number of mucros, this type is further divided into four groups (Klaus, 1980, 1989), among which the perexcentromucronate umbos, having one mucro excentrically positioned near the upper edge of the umbo, is the most similar to *P. prekesiya* (Plate I, 4, 5).

In his survey of the external morphology of ovulate cones in *Pinus*, Klaus (1980) listed six species with perexcentromuronate umbos in sect. *Pinus*, viz. *P. kesiya*, *P. massoniana* Lambert, *P. resinosa* Aiton, *P. brutia* Tenore, *P. halepensis* Miller and *P. pinea* L.. This survey, however, did not include five species in sect. *Pinus*, such as *P. hwangshanensis* Hsia, *P. luchuensis* Mayr, *P. taiwanensis* Hayata, *P. uncinata* Miller ex Mirbel and *P. yunnanensis* (Price et al., 1998). We checked the umbo types of all the species in subgenus *Pinus* in the collections in the herbarium at KUN and published accounts, such as the monograph of Farjon (2005) and the Gymnosperm database (Earle, 2008). We could confirm that the perexcentromucronate umbos is only present in sect. *Pinus* (Price et al., 1998) and only seven extant pines in this section have perexcentromucronate umbos. It is

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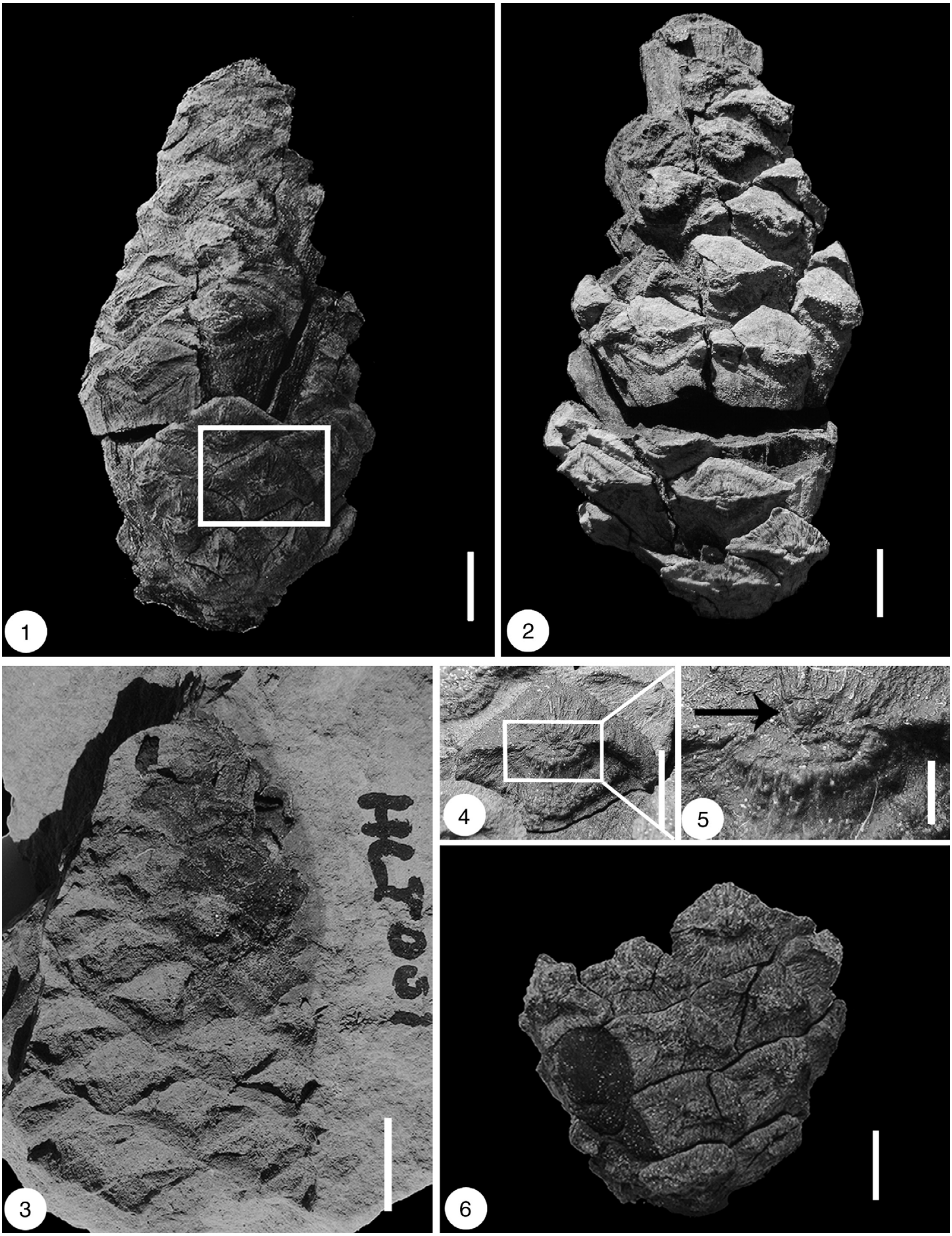
Plate I. The ovulate cone and the mold of *Pinus prekesiya* sp. nov. Scale bar = 1 cm in Figs. 1–4, 6 and 0.1 cm in Fig. 5.

1, 2.	Holotype (specimen no. HLT 001A), showing the three dimensionally preserved complete cone.
3.	Mold of holotype (specimen no. HLT 001B).
4.	Close-up of a basal apophysis from a lower portion of the holotype (in the white rectangle of HLT001A), showing the transverse keel, dorsal umbo in the center and the sealing band located in the lower portion of the apophysis. Note that the apophysis bears numerous ridges radiating from the umbo, on which a short and curved mucro appears in the upper field of umbo above the transverse keel.
5.	Close-up of an umbo from the apophysis of Plate I, 4 (in the white rectangle), showing the perexcentromucronate umbo (arrow) and the presence of vallum on the lower part of the umbo.
6.	Paratype (specimen no. HLT002).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therefore suggested that *P. prekesiya* can be assigned to sect. *Pinus*. To understand the taxonomy of *P. prekesiya*, a comparison with both extant and fossil pine cones is made.

4.1.1. Comparisons of P. prekesiya to extant cones

There are seven extant pines with perexcentromucronate umbos in sect. *Pinus*. Besides the presence of perexcentromucronate umbos, *P. prekesiya* is also defined by having a vallum, a ring-like area encircling the umbo that is differentiated and distinct from it (Klaus, 1980, 1989) (Plate I, 4). This feature has not been seen in the two extant species, *P. resinosa* Aiton and *P. massoniana* Lamb. (Table 1). Strong affinities between our fossil and these two modern species can therefore be excluded. In addition, these two species differ from our fossil in their much more ovoid cone shape (Table 1). The present fossil cone has obviously transverse and radial ridges on the long rhombic and swollen apophyses (Plate I, 4, 5); however, such ridges are absent in *P. pinea* L. The apophyses in *P. pinea* are bulbous and round with smooth surface (Table 1), and therefore *P. pinea* can easily be distinguished from the *P. prekesiya*.

The two Mediterranean pines *P. halepensis* and *P. brutia* share several cone characters with our fossils (Table 1; Klaus, 1989), but they are quite different from *P. prekesiya* as their apophyses are flat, smoothly rounded and only slightly to moderately transversely keeled (Table 1), while the apophyses of *P. prekesiya* are swollen, long rhombic, obviously with transverse and radial ridges (Plate I, 1–4, 6). With regard to features such as cone size, apophyses and umbos, *P. prekesiya* falls in the range of both *P. kesiya* and *P. yunnanensis* in subsect. *Pinus* (Price et al., 1998; Table 1; Plate II, 1–4). Both *P. kesiya* and *P. yunnanensis* have two varieties, *P. kesiya* var. *kesiya*, *P. kesiya* var. *langbianensis*, *P. yunnanensis* var. *yunnanensis*, and *P. yunnanensis* var. *pygmaea* (Fu et al., 1999; Farjon, 2005). The major differences among these varieties are the needle characters. So we only focus on our comparisons at the specific level.

The total number of cone scales per cone in *P. kesiya* and *P. yunnanensis* is different, e.g. *P. kesiya* has about 60 to 80 scales and *P. yunnanensis* possesses 70–100 scales, whereas *P. prekesiya* has only about 50 of them. Moreover, the umbos of *P. prekesiya* are slightly sunken (Plate I, 4, 5), but those of both *P. kesiya* and *P. yunnanensis* are somewhat protruding (Fu et al., 1999; Erwin and Schorn, 2006). The apophyses of *P. prekesiya* obviously have transverse and radial ridges, while those of *P. kesiya* are only transversely keeled and *P. yunnanensis* cross keeled (Table 1). Also, the apophyses of *P. yunnanensis* always appear to be irregular rhombic with much rounder two upper sides than those in *P. prekesiya* (Plate II, 1, 2). Having a slightly swollen or flat upper apophysis and depressed lower apophysis (Plate II, 3, 4), *P. kesiya* is overall the most closed living representative to *P. prekesiya*. In other words, *P. prekesiya* might have affinities with *P. kesiya* and *P. yunnanensis*, but has a closer affinity with *P. kesiya*. Hence the fossil species is classified into subsect. *Pinus*.

4.1.2. Comparisons of P. prekesiya to fossil cones

As demonstrated above, the late Miocene *P. prekesiya* is assignable to subsect. *Pinus* (Price et al. 1998); therefore we restrict our comparisons to previously published Cenozoic pine cones assignable to this subsection. There are currently about fifteen fossil pine cone species documented from Eurasia and America (Table 2).

P. prekesiya has a symmetric cone, which is shared by five fossil morphospecies (Table 2). With regard to the general shape of the cones, *P. prekesiya* is comparable to *P. baileyi* Axelrod, *P. driftwoodensis* Stockey, *P. hampeana* (Unger) Heer, *P. speciosa* Li, *P. ornata* (Sternberg) Brongniart and *P. yunnanensis*. *P. hampeana, P. speciosa* and *P. ornata* are denticulatomucronate, i.e. having a long mucro positioned on the upper edge of umbo field (Table 2), whereas *P. prekesiya* is clearly perexcentromucronate. Due to its poor preservation, the fossil cone of *P. yunnanensis* fails to exhibit detailed characters for further comparison (Tao and Kong, 1973); the mucro is not well preserved and its characters cannot be seen. However, the umbos of the fossil *P. yunnanensis* are protruding, which differs from the sunken umbos of *P. prekesiya*. *P. driftwoodensis* appears not to have a mucronate and vallate umbo on the apophysis, so it can be easily distinguished from *P. prekesiya*. *P. baileyi*, on the other hand, is the most similar fossil species to *P. prekesiya* due to symmetric cone shape, similar size and perexcentromucronate umbo. *P. baileyi* is also described as similar to *P. kesiya* (Erwin and Schorn, 2006), but *P. baileyi* differs from *P. kesiya* in having a protruding and avallate umbo. In summary, our fossil cones are not assignable to any fossil species of subsect. *Pinus*.

Comparisons with both the extant and fossil *Pinus* species demonstrate that our fossil cones cannot be assigned to any of them. Therefore, we describe them as a new species, *P. prekesiya*. This new species has the closest affinity with *P. kesiya* from Southeast Asia.

4.2. Biogeographical implications

Recent molecular systematic studies indicate that *P. kesiya* and *P. yunnanensis* show a close phylogenetic affinity and they may have diverged from the same ancestor (Wang et al., 1999; Yu et al., 2000; Gernandt et al., 2005; Eckert and Hall, 2006). From a morphological point of view, both *P. kesiya* and *P. yunnanensis* are very similar except

Table 1
Comparisons of *Pinus prekesiya* sp. nov. to perexcentromucronate cones of the extant species assignable to sect. *Pinus* sensu Price et al. (1998).

Species	Cone shape	Cone length (cm)	Cone width (cm)	Apophyses in middle	Umbo	Vallate	Keel type	Geographic location	References
P. prekesiya sp. nov.	Ovoid to conical	6.0–7.7	3.0–3.5	Long rhombic, swollen	Slightly sunken	Yes	Obviously transversely and radially ridged	Central Yunnan, China	
P. brutia	Broad conical	(4–)6–10 (–12)	4.0–5.0	Smoothly rounded, flat	Flat to slightly raised	Subvallate	Slightly to moderately transversely keeled	Mediterranean Basin	Silba (1986)
P. halepensis	Broad conical	6.0–12.0	4.0–5.0	Smoothly rounded, flat	Flat to slightly raised	Yes	Slightly to moderately transversely keeled	Mediterranean Basin and W Asia	Silba (1986)
P. kesiya	Ovoid	5.0–7.0 (10)	4–5 (open)	Rhombic, swollen	Slightly sunken or protruded	Yes	Obviously transversely keeled	SE Asia	Fu et al. (1999)
P. massoniana	Ovoid, conical-ovoid, ovoid-cylindric	(2.5) 4–7	2.5–4 (5)	Rhombic, slightly swollen or flat	Flattened, slightly sunken	No	Slightly transversely keeled	China	Fu et al. (1999)
P. pinea	Broad ovoid to globose	8–12 (15)	5–11 (12)	Bulbous, smoothly rounded	Raised	Yes	No	Mediterranean Basin	Silba (1986)
P. resinosa	Ovoid to conical	4.0–6.4	3.0–3.5	Slightly raised	Centrally depressed	No	Slightly transversely keeled	NE America	Silba (1986)
P. yunnanensis	Conical-ovoid	3.0–7.0 (10)	4.0–5.0 (open)	Rhombic, swollen	Slightly sunken or slightly protruded	Yes or No	Cross keeled	SW China	Fu et al. (1999)

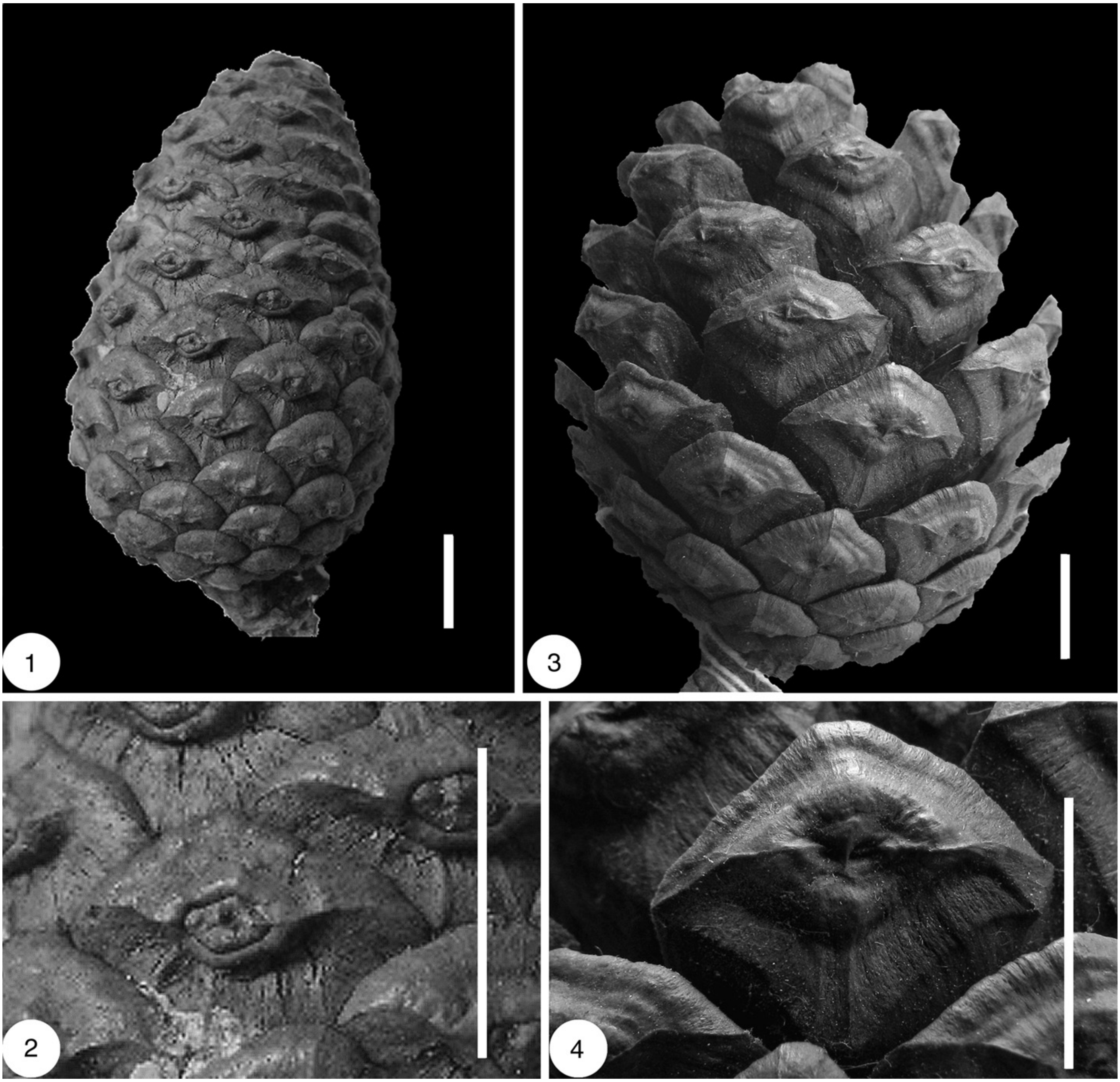

Plate II. The extant ovulate cones of *Pinus yunnanensis* and *Pinus kesiya* from KUN for comparison. Scale bars = 1 cm.

1, 2. Ovulate cone of *Pinus yunnanensis* (XYW 110).
1. Cone.
2. Close-up of an apophysis from the middle part of the cone in Fig. 1, showing the presence of a perexcentromucronate umbo and a transverse ridge.
3, 4. Cone of *Pinus kesiya* (XYW 130).
3. Cone.
4. Close-up of an apophysis from the middle part of the cone in Fig. 3, showing the presence of a perexcentromucronate umbo and a transverse ridge.

small differences in needle and cone morphology (Fu et al., 1999; Table 1). Because *P. prekesiya* shows a combination of characters found in both ovulate cones of *P. kesiya* and *P. yunnanensis*, it is suggested that *P. prekesiya* might have represented the ancestral stock of these two species. In her review of extensive fossil records from the Northern Hemisphere, Millar (1998) hypothesized that *P. kesiya* could have derived from an Eocene southern refugia lineage, whereas *P. yunnanensis* might have evolved from an Eocene mid-latitude refugia lineage. Eckert and Hall (2006) studied the phylogeny, historical biogeography, and patterns of diversification of *Pinus* and pointed out that *P. kesiya* and *P. yunnanensis* may have diverged in the early Pliocene based on molecular clock data. Both the molecular dating (Eckert and Hall, 2006) and the presence of *P. prekesiya* in the late Miocene suggest that the divergence between *P. kesiya* and *P. yunnanensis* might have taken place during the Neogene. This is in conflict with Millar's hypothesis, and therefore refutes it. The divergence of *P. kesiya* and *P. yunnanensis* might have been triggered by the continuous uplift of the Tibetan Plateau and global cooling

Table 2
Comparisons of *Pinus prekesiya* sp. nov. to three dimensionally preserved Neogene ovulate cones assignable to sect. *Pinus* sensu Price et al. (1998).

Species	Cone shape	Cone symmetric	Cone size	Umbo	Mucro (-mucronate)	Vallate	Age	References
P. prekesiya sp. nov.	Ovoid-conical	Yes	6.0–7.7 × 3.0–3.5 cm	Flat, slightly sunken	Perexcentro-	Yes	Late Miocene	Present study
P. arnoldii	Long conical	?	5–7 × 1.8–2.8 cm	Protruding	No	No	Eocene	(Miller, 1973; Stockey, 1984)
P. baileyi	Conical to oblong	Yes	5–6 × 2.5 cm	Protruding	Perexcentro-	No	Mid Eocene / early Oligocene	Erwin and Schorn (2006)
P. brevis	Ovoid	No	Up to 6 cm long	Sunken	Erectoexcentro-	Yes	Pliocene	Mai (1986)
P. dixoni	Long ovoid to cylindrical	No	Up to 13 cm long	Sunken	Denticulato-	Yes	Late Miocene	Mai (1986)
P. driftwoodensis	Cylindrical	Yes	3–4 × 2.7 cm	Protruding	No	No	Mid Eocene	Stockey (1983)
P. engelhardtii	?	No	Up to12 × 7.5 cm long	Protruding	Centro-	No	Miocene	Mai (1986)
P. hampeana	Long ovoid	Yes	4–8 cm long	Flat, slightly sunken	Denticulato-	Subvallate	Mid Miocene	Mai (1986)
P. nodosa	Ovoid	No	Up to 6.5 × 4 cm long	Sunken	Denticulato-	Subvallate	Early Miocene	Mai (1986)
P. ornata	Ovoid	Yes	< 9 cm long	Flat	Denticulato-	Vallate	Oligocene, Miocene	(Mai, 1986; Teodoridis and Sakala, 2008)
P. parabrevis	Pointed ovoid	No	Up to 5 × 2 cm	Sunken	Excentro-	No	Late Miocene	Mai (1986)
P. princetonensis	Cylindrical	?	4–4.8 × 1.5–2 cm	Protruding	No	No	Mid Eocene	Stockey (1984)
P. salinarum	Ovoid	No	5.2–8.5 × 4.7 cm	Protruding	Perexcentro-	No	Mid Miocene	Mai (1986)
P. speciosa	Elliptic	Yes	6.4 × 3.4 cm	Sunken	Denticulato-	No	Miocene	NIGMR (1982)
P. spinosa	Long ovoid to elongate	No	Up to 14 cm long	Protruding	Centroerecto-	No	Late Eocene to Pliocene	Mai (1986)
P. urani	Broadly ovoid to cylindrical	No	Up to 9 cm long	Sunken	Denticulato-	No	Mid to late Miocene	Mai (1986)
P. yunnanensis	Oblong	Yes	4.5–5.5 × 2.5 cm	Protruding	?	?	Late Pliocene	Tao and Kong (1973)

trend in the late Neogene: one adapted to drier climate and evolved to *P. yunnanensis*, while the other survived in a more southern and humid region and differentiated to *P. kesiya.*

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